

THE RELATION BETWEEN HEARING AND FLYING IN CRICKETS¹

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ABSTRACT: Hearing and flying are closely coupled functions in true crickets (Grylloidea). Although the auditory tympana have been lost many times independently in crickets, they are virtually never lost in species that can fly. Since crickets migrate at night it seems likely that tympana are retained to avoid bat predation.

The ancestor to modern crickets (Grylloidea) probably possessed tibial auditory tympana and tegminal stridulatory devices similar to those of modern species. Subsequently the stridulum (and therefore acoustical communication) has been lost many times. In Australia, for example, where 103 species (or 18.9% of the known fauna) lack a stridulum, the stridulum was lost at least 27 times. In Africa it was lost at least 17 times. It was lost a number of times on Pacific islands as well (i.e. New Caledonia, Hawaii, Fiji, and Lord Howe — Otte, Alexander and Cade 1988, Otte and Rentz 1985, Otte and Rice in prep.)

Although the stridulum has not been lost in any United States species, calling behavior has been lost in at least seven species (*Gryllus ovisopis* [Gryllinae], *Oligocanthopus prographus* [Mogoplistinae], *Tafalisca lurida* and *Hapithus brevipennis* [Eneopterinae], *Falcicula hebardi* [Trigoniinae], *Scapteriscus abbreviatus* [Gryllotalpinae] and northern populations of *Hapithus agitator* [Eneopterniae]) (Walker 1974). Absence of a calling song must be a precursor to the loss of the stridulum; therefore examination of these species should give one clues as to the selective forces causing muteness and deafness.

Walker (1974) notes also that *Gryllus fultoni* on Key Largo lacks a functional calling song. And in the sibling pair *Hapithus melodius* and *H. brevipennis*, the former species retains both calling and courtship songs, while the latter has never been heard to produce either song, even though it appears to have a functional stridulum.

The circumstances which cause non-acoustical methods of communication to entirely replace acoustical modes is open to speculation. Do acoustical signals lose their directionality, and therefore effectiveness, in certain situations (caves, burrows), or become ineffective in the presence of noise (sea shores), or less effective than other modes of signal transmission (pheromones, substrate vibration, visual signals) under certain circumstances (burrows, caves, or on grasses)?

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Walker (1974), noting that all U.S. mute species are flightless, speculates that muteness is associated with their higher degree of sedentarieness: "Sedentary populations characteristically occupy relatively permanent habitats and are not subject to the extreme fluctuations in density of breeding adults characteristic of temporary habitats. Consequently, chance encounters or short-range signals become more dependable pair-forming techniques." He suggests two other possible causes: acoustically orienting predators could select against singing males; or the loss of song could evolve if it caused reduction in interbreeding with a closely related species possessing a nearly identical song (as may have happened to *Gryllus ovisopis* when it speciated from *G. fultoni*).

In Australia mute species are best represented among the following groups: a) burrowing crickets from rain-forests and open woodlands (most belong to the genus *Apterogryllus* [Brachytrupinae] and all probably derive from a single mute and wingless ancestor); b) crickets inhabiting lush grasses along water courses (all are small Trigonidiinae, but the stridulum may have been lost 3 or 4 times in this group); c) crickets inhabiting canopy foliage in rain forest or seasonally wet woodland (these belong to three groups: Trigonidiinae (*Amusurgus*, *Metiochodes*, *Cyrtoxiphoides*); Podoscirtinae (*Mundeicus*, *Aphonoides*); and Pentacentrinae); d) crickets inhabiting seasonally moist grasslands (Euscyrinae — probably lost at least twice); e) crickets inhabiting ant nests (Myrmecophilinae — muteness probably evolved but once in this group, perhaps outside Australia); f) forest floor (leaf litter) species (Nemobiinae and Phalangopsinae — stridulum perhaps lost three times in the Nemobiinae and two or three times in the Phalangopsinae); g) shore-inhabiting species (Nemobiinae, *Apteronemobius* — since this genus is widespread over the Pacific ocean, the stridulum may have been lost outside Australia); (h) cave-inhabiting species (Nemobiinae, *Nambungia*).

A survey of the Australian crickets shows that auditory tympana are often retained *after* the tegminal stridulatory mechanism is lost, that is, they continue to hear after becoming mute (*Amusurgus*, *Metiochodes* [Trigonidiinae] *Pentacentrus* [Pentacentrinae] *Mundeicus*, *Umbulgaria*, *Aphonoides*, [Podoscirtinae], *Euscyrus*, and *Patiscus* [Euscyrinae]. Partial loss of the stridulum is seen in *Hemiphonus*, *Unka* (Podoscirtinae), *Trigonidomorpha* (Trigonidiinae) and *Merrinella* (Euscyrinae). Since a loss of the sound producing mechanism is probably usually accompanied (or followed) by a loss in the listening mechanism, one must presume that some kind of selection pressure opposes the loss of a tympanum in these species.

In my survey of the Australian fauna (based on Otte and Alexander 1983) I noticed that *virtually all flying species* retain a tympanum, even those species that have lost the stridulum. The only non-hearing crickets

are ones that cannot fly. We can look at the relation between singing³, hearing⁴, and flying⁵ in the Australian fauna more closely. All the possible combinations of these three characters are shown in Figure 1 and next to them the number and the percentage of species possessing the condition. Two very common conditions occur in this fauna: A large number of species can sing, hear, and fly. But a much larger number of species can sing and hear, and are flightless (B). Of the remainder, 57 species (or 20% of the total) cannot fly, cannot hear and cannot sing (H); 46 species (10%) cannot sing but can both fly and hear (D). Notice that two of the possible combinations have no representative species: There are no species which can sing and fly but cannot hear (C) and there are no mute and deaf species which can fly (G). Condition C may be absent for two reasons: a) Perhaps a species which cannot hear will not retain its song mechanism. This is probably true in most cases, but rare instances do occur in which males continue to sing even though a stridulum is lost (as in condition F — Evans 1988). b) The condition is rare because flying species are selected against if they are deaf. The latter reason is probably true, given that there are no species which can fly *and* which cannot also hear (see also condition G).

Few species have conditions E and F; both conditions are probably transitional between B and H. Outside Australia I know of no species with either of these conditions. Of the four Australian species which have lost the stridulum but retain the tympanum, one species has a tiny, apparently rudimentary, organ; another species is geographically variable with western Australian specimens retaining a tympanum, and eastern Australian ones having lost it (perhaps in this species occasional individuals are macropterous).

Condition F, in which the stridulum is retained in a species that has lost its tympana, is also exceptional. Fortunately the acoustical behavior of one of these species is known. Males of *Balamaro gidyia* have a peculiar mode of signalling (Evans 1988). In the presence of females they tap the grass on which they rest with the abdomen, presumably transmitting information to the females through vibration of the substrate. Males tap in pairs, and during the first tap of each pair they stridulate. We do not know what *B. gidyia*'s nearest relatives do. *B. marroo* possesses both a stridulum and well-developed tympana. *B. albovittata* from eastern Australia has no stridulum and no tympana; in western Australia this species has no stridulum but retains a small tympanum. We speculate that in the lineage leading to *B. gidyia* males called females by stridulating; later, males began to vibrate the substratum (grass blades on which both were

³have a tegminal stridulatory mechanism

⁴have a tibial auditory tympanum

⁵possess long hind wings

perched) during stridulation; gradually tapping began to predominate as the information carrier, and tympana were lost when the acoustical component of the signal disappeared; the stridulation now heard faintly during the first tap is perhaps a vestige of the original call. Once it disappears, as it may already have done in *B. albovittata*, the stridulum may also be lost.

One is led to conclude that hearing is important to flying crickets.

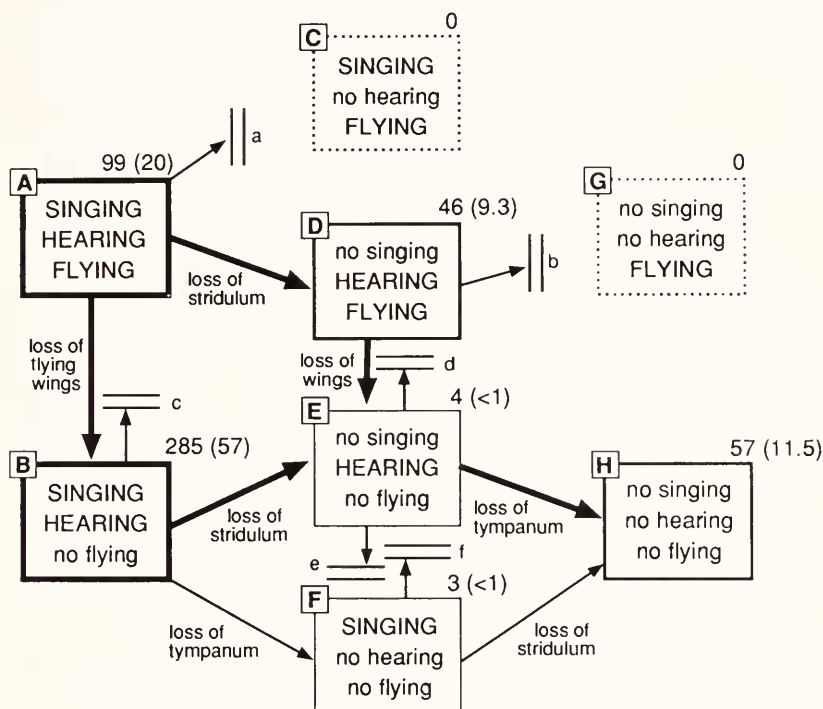


Figure 1. All possible combinations of singing, hearing, and flying in the known Australian cricket fauna. *Singing* means possession of a stridulatory mechanism; *hearing* means possession of a tibial auditory tympanum; *flying* means possession of hind wings long enough to make flight possible. Numbers in the upper right indicate the number (and percentage) of species possessing the condition. Arrows indicate the presumed direction of evolutionary change. Parallel lines indicate evolutionary transformations which have probably not occurred — *a* and *b* because absence of hearing in flying species is perhaps strongly selected against by bats or other predators; *c*, *d*, *e*, and *f* because once a particular complex mechanism is lost it is highly unlikely to evolve again. Conditions E and F are absent in African and other faunas, suggesting that the transition from B or D to H is rapid.

Africa and Pacific island crickets hold to this pattern precisely, though we have discovered a single species of *Adenopterus* (Loyalty Islands) which possesses long hind wings and lacks tympana (Otte, Alexander and Cade 1987).

The association between hearing and flying is also evident within some Australian species which show developmental flexibility in both characteristics — further confirming a functional coupling between them. *Euscyrtus hemelytrus* (Euscyrtinae) always possesses tympana, but the outer tympanum is sometimes obsolete in micropterous specimens. In general, macropterous individuals have larger tympana. We noted the following variation in this species (Otte and Alexander 1983): Micropterous individuals are quite variable, with the outer tympanum sometimes obsolete and represented only by a dimple. Macropterous males had very large and conspicuous inner and outer tympana. A macropterous male and female from Upper Burma have very large inner and outer tympana, but a micropterous female has inner and outer tympana barely visible. A micropterous female from Manila, Philippines has an outer depression and a conspicuous inner tympanum. Two micropterous males and a female from Assam (Bangladesh) have an inner tympanum and the other tympanum represented by a dimple. Four other females from the same place are macropterous and have large inner and outer tympana.

Metioche vittaticollis (Trigonidiinae) are similar to *Euscyrtus*. Macropterous individuals possess large tympana, while micropterous individuals have either small inner and no outer tympana, or small outer and larger inner tympana, or no tympana at all. Of 61 individuals examined only the 45 macropterous individuals had prominent inner and outer tympana.

We also noted dimorphism in wings and tympana in *Trigonidomorpha sjostedti* (Otte and Alexander 1983). In this species wingless males and females usually have small dimples instead of tympana; occasionally a small inner tympanum is visible. Evans (1988) has further studied wing length and tympana in this species. She crossed the two phenotypes (winged/ +tympana and wingless/ -tympana) and found that the dimorphism does not result from a simple Mendelian 1-locus, 2-allele mechanism, since all crosses produced both phenotypes in both sexes. Field collected wingless/-tympana adults produced winged/+tympana offspring. She also found that both morphs possessed tympanal organs with well developed scolopidia, attachment cells, and accessory cells, in close proximity to the anterior tympana trachea; but the tympana of the wingless morph were hidden beneath a layer of cuticle.

Several experimental studies have shown that crickets can hear bat sounds and take evasive action in the presence of bat sounds (Griffin 1958, Popov and Mrkovich 1982, Moiseff and Hoy 1983, Nolen and Hoy 1984, Doherty and Hoy 1985).

It has also been suggested that the development of receptors sensitive to aerial sounds may have been favored by selection if they enabled individuals to stay within a dispersing group by responding to the flight sounds of conspecifics (Evans 1988, and references therein).

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